PREDATION RISK ASSOCIATED WITH GROUP SINGING IN A NEOTROPICAL WOOD-QUAIL

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ABSTRACT.—Decades of fruitful research on the study of vocal communication in birds have provided surprisingly little evidence of a predation cost associated with singing. In this paper, I report the first observational evidence of a risk of predation associated with chorusing in a Neotropical wood-quail. Black-breasted Wood-Quail (*Odontophorus leucolaemus*) live in groups year-round and produce coordinated group choruses or duets. Three mammalian and two avian species of predators were attracted to playbacks of recorded wood-quail choruses that I used during population surveys and capture attempts from March to August, 2000–2002. The trade-off between signaling and predation risk may be an important force in the evolution of chorusing in New World quails. *Received 12 February 2004, accepted 19 July 2004.*

Long distance vocalizations are used for territory defense, mate attraction, and other functions in a variety of animals (Bradbury and Vehrencamp 1998, Todt and Naguib 2000). Whenever such signals are sent, however, there is a danger that they will be heard and taken advantage of by illegitimate receivers, such as competitors, parasites, or predators (McGregor 1993, Bradbury and Vehrencamp 1998, Haynes and Yeargan 1999). For example, the parasitoid tachinid fly, *Ormia ochracea*, is attracted to tape recordings of a host cricket, *Gryllus integer* (Cade 1975); the fringe-lipped bat (*Trachops cirrhosus*) uses acoustic cues to capture calling frogs (Tuttle and Ryan 1981); and several species of foliage-gleaning bats in Panama use the mate-attracting songs of male katydids to locate these prey (Belwood and Morris 1987). In birds, however, evaluation of predation costs associated with signaling has primarily been restricted to studies of plumage conspicuousness (Gotmark 1992, Promislow et al. 1992, Andersson 1994). Although most studies of costs associated with vocal communication in birds have focused on energetics (Eberhardt 1994, Oberweger and Goller 2001, Thomas 2002), eavesdropping by predators has been demonstrated experimentally in three species. The first experimental evidence comes from a study of Red-winged Blackbirds (*Agelaius phoeniceus*), in which nests accompanied by playback of female 'chit' calls were depredated at higher rates than nests without playback

(Yasukawa 1989). Two recent studies provide additional experimental support: Brown Skuas (*Stercorarius antarctica*) use the mate attraction calls of colonially nesting seabirds as a cue for prey location and selection (Mougeot and Bretagnolle 2000), and long-distance calling in Crested Tits (*Parus cristatus*) increases the risk of predation by Eurasian Sparrowhawks (*Accipiter nisus*; Krams 2001).

In this study, I report observational evidence that predators are attracted to group singing in Black-breasted Wood-Quail (*Odontophorus leucolaemus*), a social species restricted to the remaining highland forest of Costa Rica. Black-breasted Wood-Quail live in coveys year-round (2 to 15 individuals) in the dense understory of cool, wet forest between 900 and 1,600 m elevation. Nesting usually occurs around the onset of the rainy season in May and June (McDonald and Winnett-Murray 1989; AMH pers. obs.). Coveys defend group territories and produce coordinated group choruses or duets. Neighboring coveys are most often heard calling back and forth just after dawn. All members of the covey participate in the chorus, and individuals often hop up on perches (dead fallen trees) approximately 1 m off the ground while singing. Depending on the weather and terrain, the chorus is audible to humans from a distance of 200–500 m (AMH pers. obs.). Because choruses and duets by a single mated pair have the same basic structure in Black-breasted Wood-Quail, hereafter I will refer to both as choruses.

METHODS

The study area is located in Monteverde (10° 15′ N, 84° 46′ W), a 1,500-ha dairy farm-

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ing community at an elevation of 1,350–1,500 m on the Pacific slope of the Cordillera de Tilarán in Puntarenas Province, Costa Rica. This area is the site of long-term ecological studies and has been well described (Nadkarni and Wheelwright 2000). Monteverde is a fragmented landscape, composed of open pastures, some cultivated bananas and coffee, and considerable remnant pre-montane and lower montane moist/wet forest (Holdridge 1967). The community lies on a narrow plateau bounded on the north by human dwellings and agriculture, on the south and west by cliffs, and on the east by a large expanse of cloud forest—the 28,000-ha Monteverde Reserve Complex, Costa Rica's largest intact highland forest. Black-breasted Wood-Quail inhabit the large windbreaks and patches of remnant forest in the Monteverde community and the continuous forest of the Monteverde Reserve Complex. Although locally common in the Monteverde area, Black-breasted Wood-Quail are generally rare throughout Costa Rica (Stiles and Skutch 1989, Fogden 1993), and are classified as a species of conservation concern by the IUCN—World Conservation Union (Collar et al. 1994, Fuller et al. 2000). In Monteverde, average covey size is four adults with approximately 77% of surveyed coveys containing three or more adults (n = 151 coveys). Average density is one covey per 3.3 ha (AMH unpubl. data).

From March through August, 2000–2002, I conducted wood-quail surveys in the Monteverde area by using playbacks of choruses to simulate territorial intrusions. A single recording from the *Indicator Birds of the Costa Rican Cloud Forest* CD (Ross et al. 1997) was used in 2000 and 2001. This 58-sec recording consisted of three choruses from a bout of counter-singing between two coveys of unknown size. The recordings used in 2002 were obtained from songs provoked by the use of playback. Recordings were made from 64 bouts of singing by 45 coveys; I used a Sony Cassette Recorder TC-D5M and Audio-Technica unidirectional microphone (70–18,000 Hz). Digital sound files were created from the analogue recordings at 22.05 kHz with 16-bit accuracy using Syrinx Version 2.2b (2001). Sixteen experimental tapes, consisting of one chorus each from 16 coveys of known size (range 2–7 adults), were made to determine whether wood-quail coveys adjusted their responses to playbacks based on the number of individuals in the "intruding" covey. These 16 choruses were chosen based on the clarity of the recording and the absence of other sounds, including singing by other species, wind, and rain. One of these tapes consisted of a 15-sec chorus that was looped to make a 30-sec recording, while each of the other tapes consisted of a single chorus lasting 26–31.5 sec.

To simulate territorial intrusions, I entered a group's territory and played a recording (30 sec from the cloud forest CD recording in 2000 and 2001, or one of the experimental tapes in 2002) using a Sony walkman, a 20-watt RMS power amplifier, and a 12.5-cm, 15-watt Speco loudspeaker (300–15,000 Hz) placed 0–2 m above the forest floor. If the group responded immediately, either by calling or approaching the loudspeaker, I did not continue with playback. If the group did not respond, I repeated the playback once every 3 min for a maximum of 15 min. Amplitude level of the playback was matched by ear to singing wood-quail and was held constant throughout the trials. In general, the playback was just loud enough so that the sound traveled approximately 200 m and was not distorted. Wood-quail coveys tended to respond immediately when a recording was played within their territories; they would sing and approach within a few cm of the loudspeaker. Solitary individuals also responded to playbacks by singing, but did not closely approach the sound source. I also used playbacks to lure wood-quail into mist nets or large traps for individual marking and genetic sampling. The number of times the recording was played during capture (from 1 to approximately 20 times per hr) depended upon the response of the focal group and the number of group members captured.

RESULTS AND DISCUSSION

Wood-quail choruses are rushing gabbles of notes patterned into two sets of paired syllables that are repeated over and over. Choruses last 10–60 sec and occur most often just after dawn (54% of spontaneous choruses occurred between 05:30 and 06:30 GMT-6, n = 87 choruses). The majority of choruses are answered by neighboring groups, and bouts of counter-

singing among neighbors last from about 1 min to over 1 hr (AMH unpubl. data). When two or more social groups come into contact near a territorial boundary, each group produces a well-coordinated chorus and the groups will either alternate or overlap their bouts of singing. Often, after a few bouts of counter-singing, one or more groups will retreat from the area. In other instances, the territorial encounters can last up to several hr. In addition to continued singing during territorial encounters, individuals produce several other vocalizations and participate in strutting displays, chases, and even physical fights with neighboring group members. Wood-quail coveys responded to simulated territorial intrusions with either choruses or approaches during 65% of surveys and 75% of capture attempts in 2000–2002 (n = 467 surveys and n = 122 capture attempts).

During surveys and capture attempts, I witnessed eight instances of predator response to playbacks of wood-quail choruses (three in 2000, four in 2001, and one in 2002). During 109 survey mornings (mean = 4.3 social groups surveyed per morning), the loudspeaker was approached by a single predator on four occasions: two gray foxes (*Urocyon cinereoargenteus*) and two Collared Forest-Falcons (*Micrastur semitorquatus*). These predators approached the loudspeaker after the recording had been played from one to three times. During 95 capture mornings, the loudspeaker was approached on three occasions by a single predator, one margay (*Leopardus wiedii*), one Barred Forest-Falcon (*Micrastur ruficollis*), and one Collared Forest-Falcon, and on one occasion by two domestic dogs (*Canis familiaris*; which have been observed to capture wood-quail in this area). While the forest-falcons approached the loudspeaker after the recording was played just three times during capture attempts, the margay and dogs responded after the recording had been played approximately 10 times. In each of these instances, the behavior of the predator suggested that it was responding to the vocalizations rather than something else in the environment. The two foxes walked directly to the loudspeaker before leaving the area upon seeing me; the margay broke through the mist nets and pounced on the loudspeaker; one Collared Forest-Falcon landed within a few m of the

approaching covey and pursued the quail on foot as they ran for cover; two Collared Forest-Falcons and the Barred Forest-Falcon perched on a branch located approximately 3 m above the loudspeaker and visually searched the immediate area; and the dogs ran directly at the loudspeaker before pausing and searching the surrounding area. Two of these predators are forest specialists (Collared Forest-Falcon, margay) and may be constrained to using vocal cues to locate prey. Unlike the other predators, the Barred Forest-Falcon is too small (165–200 g; Stiles and Skutch 1989) to capture adult wood-quail (mean = 295 g ±16 SD, n = 103 adults; AMH unpubl. data); however, because these playback trials occurred during the wood-quail breeding season, it may have been looking for chicks.

Although energetic costs associated with producing signals have received the most attention, there is increasing evidence that additional costs, such as increased exposure to predators, should also be considered in studies of the evolution of communication (reviewed in Gil and Gahr 2002). This may be particularly important in birds because the empirical evidence for a high energetic cost of singing in passerines is equivocal (Eberhardt 1996, Gaunt et al. 1996, Oberweger and Goller 2001, Thomas 2002, Ward et al. 2003), and studies of a nonpasserine, Red Junglefowl/domestic roosters (*Gallus gallus*), show that crowing is not energetically costly (Chappell et al. 1995, Horn et al. 1995). Similarly, chorusing in Black-breasted Wood-Quail seems unlikely to be energetically costly even though it is a year-long endeavor: on any given day, individuals sing for a short amount of time, perhaps giving only several bouts, each less than 1 min in length (AMH unpubl. data). This is in contrast to the high level of singing effort, in terms of both frequency and duration of songs, observed in many male passerines during the breeding season (Welty 1982, Catchpole and Slater 1995). This comparison suggests that a high metabolic cost and loss of time that could be spent foraging or resting are not likely for wood-quail, with the exception of chorusing associated with prolonged territorial encounters.

The observations presented here suggest that predators eavesdrop on choruses produced by wood-quail. In my study area, a

predator responded to recordings on 1.4% of the 589 surveys or capture attempts. This is likely to be a great underestimate of the risk of predation; it is reasonable to presume that I did not see all of the predators that were attracted to the playbacks, in part because they avoid humans. Moreover, the suite of detected predators included both those that are commonly seen (e.g., Barred Forest-Falcon, gray fox) and those that are observed only rarely in the Monteverde area (e.g., Collared Forest-Falcon, margay) (Fogden 1993, Nadkarni and Wheelwright 2000). Detection of these rare or uncommon predators provides further support that the potential suite of predators is large and that chorusing in Black-breasted Wood-Quail may have a non-trivial cost of predation. Additional anecdotal evidence suggests that the risk of predation associated with chorusing will be even greater during territorial encounters because of increased amounts of singing and impaired vigilance. In the few cases in which I was able to closely observe territorial encounters, I successfully approached the wood-quail to within a few m without being detected. Future playback studies should reduce variation in the amount of signal that is available to potential predators from one playback trial to the next, and incorporate a control (i.e., recordings of silence or other sounds) to account for the likelihood of detecting a predator by chance. These modifications would improve the estimate of the frequency of eavesdropping and confirm its relative importance in this system.

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